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A NEW SPECIES OF *MESOCLEMMYS*, FROM THE OPEN FORMATIONS OF NORTHEASTERN BRAZIL (CHELONII, CHELIDAE)

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ABSTRACT

A new species of South American side-necked turtle is described from the state of Piauí, Brazil. It is related to the Amazonian species of the genus Mesoclemmys s.l. (new acception) and is apparently a biogeographically relictual population of a species formerly living under a more humid climate in northeastern Brazil.

KEYWORDS: Chelonii, Chelidae, systematics, taxonomy, phylogeny, *Mesoclemmys perplexa*, new species, Piauí, Brazil.

INTRODUCTION

Systematic knowledge of the Chelids (Chelidae), a turtle family widely distributed in the Australian and the Neotropical realms, is still progressing, with new species being brought to light sporadically. Among South American chelids, the genus *Phrynops* Wagler, 1830 (s.l.) is the least resolved taxonomically. A recent revision by McCord *et al.* (2001) recognizes six genera: *Phrynops* Wagler, 1830, *Rhinemys* Wagler, 1830, *Mesoclemmys* Gray, 1863, *Batrachemys* Stejneger, 1909, *Bufocephala* McCord *et al.*, 2001, and *Ranacephala* McCord *et al.*, 2001.

According to McCord *et al.* (2001), the genera *Batrachemys* and *Phrynops* include six and four species, respectively, whereas the genera *Ranacephala*, *Rhinemys*, *Bufocephala*, and *Mesoclemmys* are monotypical. Although we agree with the specific allocations of the genera

Phrynops and *Rhinemys* proposed by these authors, we refrain to follow their taxonomic arrangements for the genera *Ranacephala*, *Mesoclemmys*, *Bufocephala*, and *Batrachemys*, which seem to be mainly based on two correlated characters, i.e., the width of the head and the degree of development of the 'parietal crest'.

Recent field works in northeastern Brasil revealed the existence of a previously unknown population of Chelid turtles here described as belonging to a new species attributed to the genus *Mesoclemmys*. The presence in this new species of the conspicuous external characters used by McCord *et al.* (2001) to establish the distinctiveness of *Mesoclemmys*, *Batrachemys*, *Ranacephala*, and *Bufocephala* reinforces the idea that such generic allocations are weakly supported by the morphological evidence at hand (see Appendix 3 and compare with Appendix B in McCord *et al.*, 2001). Additionally, the lack of information on the internal anatomy

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of most species of 'toad-head turtles' contribute to perpetuate poorly supported taxonomic arrangements for the group. We tested the robustness of the phylogenetic scheme proposed by McCord *et al.* (2001) by including the new species described herein. Results of this test are shown below and support the view that a more cautious taxonomic arrangement than the one proposed by McCord *et al.* (2001) should be followed for the 'toad-headed' South American chelids. From a strictly nomenclatural point of view, the use of the oldest name *Mesoclemmys* to accommodate all species currently included in the genera *Batrachemys*, *Bufocephala*, *Ranacephala*, and *Mesoclemmys* sensu McCord *et al.* (2001) represents the most appropriate decision until a more robust phylogenetic hypothesis is proposed for the group (see Appendix 1 and Discussion below).

Distribution of the Genus *Mesoclemmys*

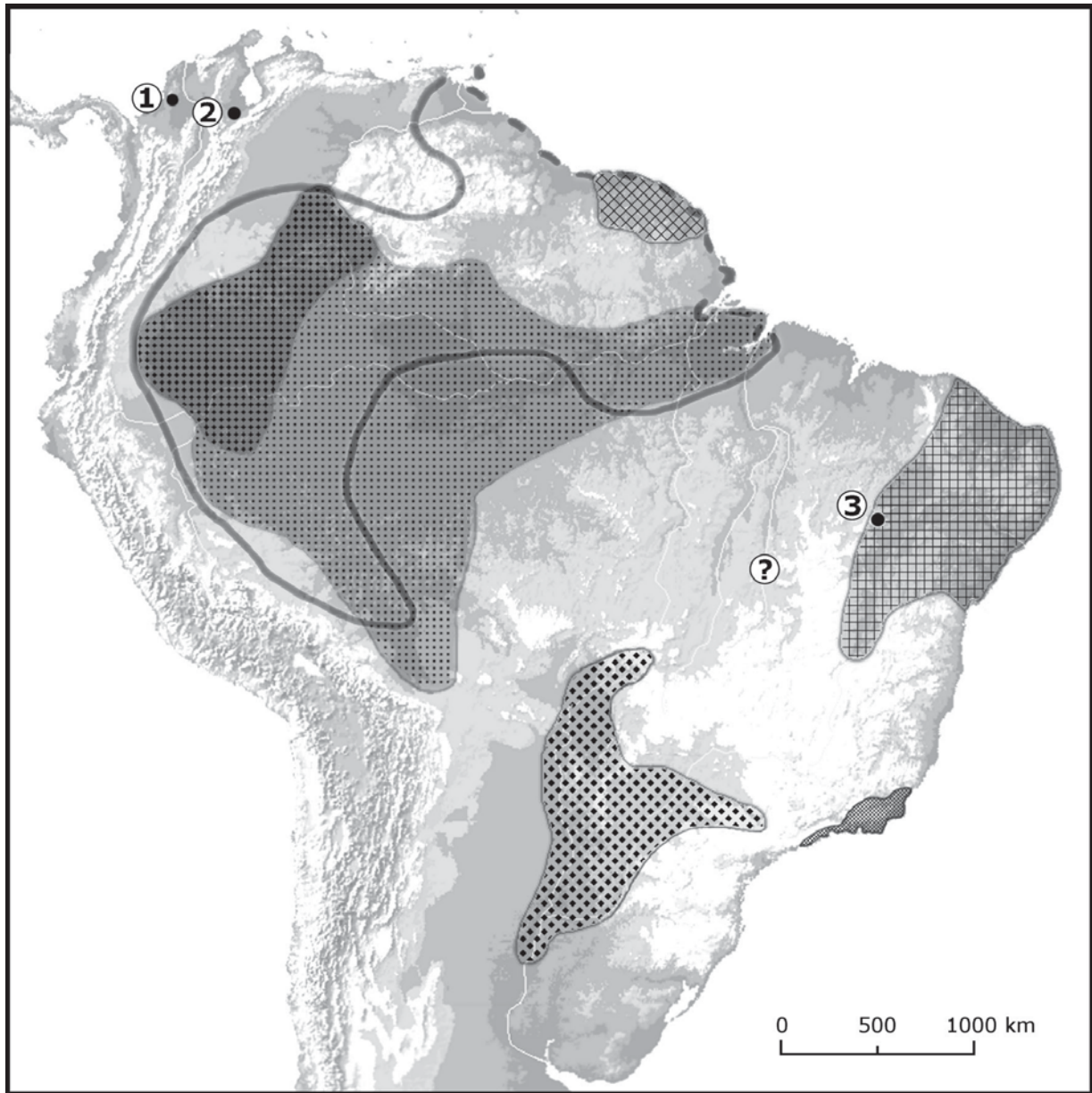
Geographical ranges of the ten species assigned here to the genus *Mesoclemmys* and discussed below are illustrated in Figure 1. *Mesoclemmys nasuta* (Guyanas), and above all *M. dahl* (Colombia) and *M. zuliae* (Venezuela), represent northern, isolated, and more or less relictual populations. *Mesoclemmys raniceps* is an Amazonian species which range extends from eastern Ecuador and Peru, northwestern Brasil, and northern Bolivia to Venezuela, and as far as the state of Pará in northern Brasil (Pritchard & Trebbau, 1984; Bour & Pauler, 1987; Iverson, 1992; McCord *et al.*, 2001). *Mesoclemmys heliostemma* is limited to the northwestern part of this range (McCord *et al.*, 2001). *Mesoclemmys gibba* has a wide distribution, rather similar to that of *M. raniceps*, with extensions on Trinidad and Guyanas (Mittermeier *et al.*, 1978; Pritchard & Trebbau, 1984; Bour & Pauler, 1987; Iverson, 1992; McCord *et al.*, 2001). Bour & Pauler (1987) noticed for *M. gibba* a geographical cline involving the color pattern, with individuals from the western part of the range (morph 'stenops' Spix, 1824) being duller than those of the eastern part (morph 'gibba'). Recently, an isolated population provisionally referred to this species has been located in the central Brazilian state of Tocantins (Maran, 2004; Vetter, 2005; Fig. 1). *Mesoclemmys hoguei*, *M. tuberculata*, and *M. vanderhaegei* are not Amazonian elements. *Mesoclemmys hoguei* is limited to the Rio Paraíba drainage in Southeastern Brazil whereas *M. tuberculata* has a northeastern Brazilian range (corresponding with the Caatinga), and *M. vanderhaegei* has a Paraguayan – central Brazilian distribution (Bour & Pauler, 1987; Iverson, 1992; McCord *et al.*, 2001). The latter two spe-

cies are superficially similar and have sometimes been confused (see, e.g., McDiarmid & Foster, 1987), despite their distinct distribution ranges.

Serra das Confusões: Type-locality of the new species

Created in October 1998, the Parque Nacional da Serra das Confusões (PNSC) is located in the south-east of the state of Piauí (08°32'–09°16'S, 43°15'–43°51'W), covering an area of 5024 km², between the towns of Caracol, Guaribas, Cristino Castro, and Tamboril do Piauí (Fig. 2). The average altitude is close to 600 m; the climate is tropical semi-arid; the biome ecosystem is Caatinga. All the area drains into the Rio Parnaíba basin. Most of the area of the park corresponds to an extensive arenitic plateau, the "Chapada dos Gerais" (locally known as "Serra Grande"), dissected by an intermittent river drainage (Rodrigues *et al.*, 2001; Zaher, 2002). The western and southern parts of the park are dominated by highly dissected rocky outcrops, forming a complex system of crevices and canyons that eventually open on lowland areas. The plateau is mostly covered by "Carrasco" vegetation (Fernandes, 2000) with an abundant leaf litter covering a sandy soil. The open lowlands, crevices, and canyons are covered by dry forest that grows on a sandy soil with small amount of leaf litter (Rodrigues *et al.*, 2001; Zaher, 2002).

H. Zaher coordinated two field trips during the years of 2000 and 2002 to the PNSC in order to survey the terrestrial vertebrate fauna (Zaher, 2002). One of the interesting results was the survey of several species with obvious Amazonian affinities, notably a new species of *Stenocercus* Duméril & Bibron, 1837 (Iguania, Tropiduridae) and an isolated population of *Vampyrus spectrum* (Linnaeus, 1758) (Chiroptera, Phyllostomidae). This new species of *Stenocercus* was only found on the plateau of the "Chapada dos Gerais", with typical "Carrasco" vegetation and dry weather during most of the year. On the other hand, *Vampyrus spectrum* was collected inside the main canyon of the rocky area called "Olho d'Água da Santa" (Rodrigues *et al.*, 2001) (Fig. 2). Here the climate is always wet and even in the hottest and driest season some waterholes remain; the temperature is rather stable. Outside these canyons, in the areas of open vegetation area, all the ponds and streams dry up during the hot season. Two species of chelid turtles were observed in association with aquatic habitats. *Mesoclemmys tuberculata* (Luederwaldt, 1926) was quite common and found nearly everywhere, includ-



- | | |
|-------------------------------------|-----------------------------|
| 1 <i>M. dahlia</i> | 3 <i>M. perplexa</i> |
| <i>M. gibba</i> | <i>M. raniceps</i> |
| <i>M. heliostemma + M. raniceps</i> | <i>M. tuberculata</i> |
| <i>M. hogei</i> | <i>M. vanderhaegei</i> |
| <i>M. nasuta</i> | 2 <i>M. zuliae</i> |

FIGURE 1. Schematic range of the recognized species of *Mesoclemmys* (from Bour & Pauler, 1987; Iverson, 1992; McCord *et al.*, 2001). Interrogation mark represents an isolated population of *Mesoclemmys* cf. *gibba*.

ing in the 'core area' of the park. That is because of its propensity to wander from one aquatic system to another, possibly at night (Vanzolini *et al.*, 1980), and to bury itself during the dry time of year, a vital adaptation in this peculiar biome. It must be noted that this is

apparently the first time that the species has been recorded from the Rio Parnaíba basin.

The second species of chelid turtle was found only on lowland areas near the arenitic outcrops, living near and inside the perennial waterholes present at the

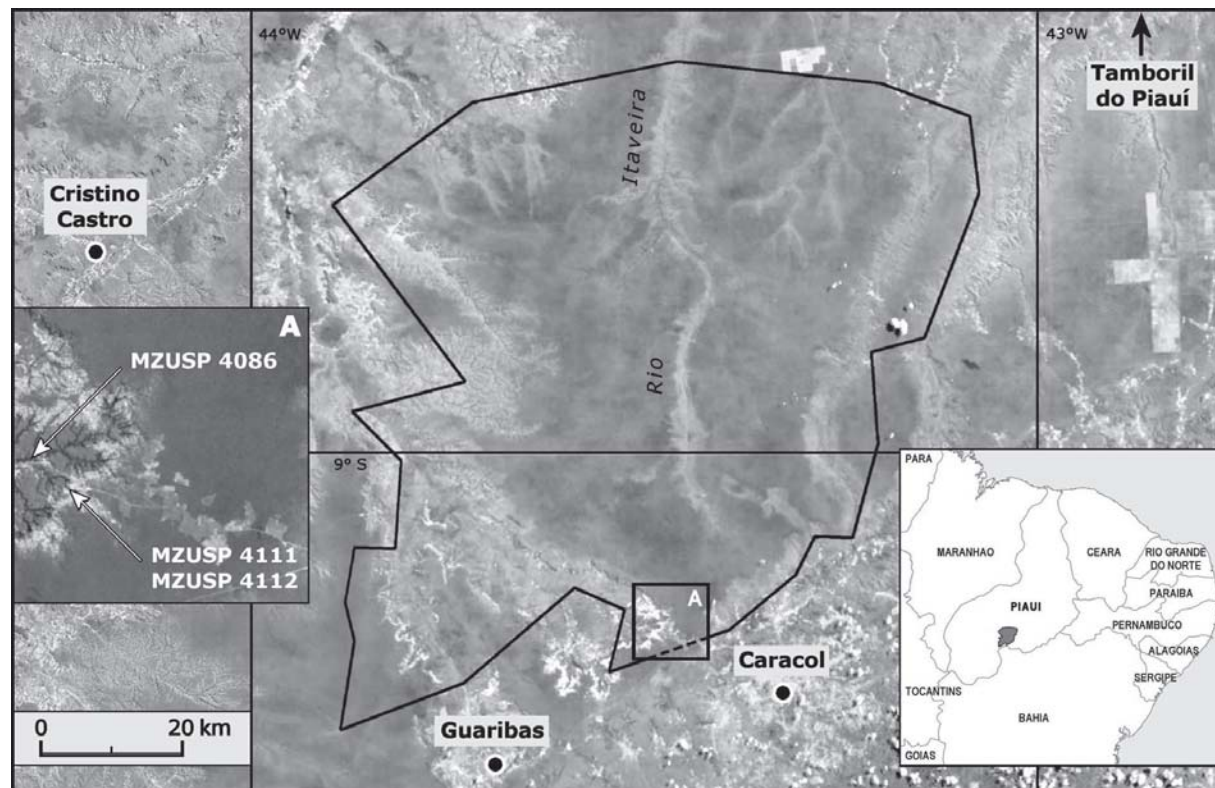


FIGURE 2. Satellite view (NASA data) of Parque Nacional da Serra das Confusões. The arrows in insert A point to the localities known as “Olho d’Água da Santa” and “Baixão do Fausto”, where the holotype and the paratypes were collected.

bottom of the canyons on the adjacent areas called “Baixão do Fausto” and “Olho d’Água da Santa (Fig. 2). Three specimens were collected. At first glance this ‘canyon turtle’ exhibited similarities with both *Mesoclemmys vanderhaegei* and *M. gibba*. A more detailed study, presently limited to the external characters, revealed that it was obviously a new species, by some features equally related to several other members of the genus *Mesoclemmys* (sensu lato). We propose to describe it as:

***Mesoclemmys perplexa* sp. nov.**

Figures 3 and 4, Table 1

Holotype: MZUSP 4111 (Museu de Zoologia da Universidade de São Paulo), a juvenile specimen (probably a female) with 67.6 mm of carapace length (see Table 1 for other measurements and Fig. 3), collected in 08 October 2000 by H. Zaher and team inside a small pond of the major canyon located in the region called “Olho d’Água da Santa”, southern part of the Parque Nacional da Serra das Confusões.

Type locality: Forested and humid areas of the regions called “Olho d’Água da Santa” and “Baixão do Fausto”,

southern part of the Parque Nacional da Serra das Confusões, State of Piauí, Brasil.

Paratypes: MZUSP 4112, a subadult female with 100.8 mm of carapace length (Fig. 4A, B), collected the same day and at the same location as the holotype. MZUSP 4086, an adult female with 193.7 mm of carapace length (Fig. 4C, D), collected in 14 January 2002 by H. Zaher and team when crossing an open area at night in the region called “Baixão do Fausto”, southern part of the Parque Nacional da Serra das Confusões.

Etymology: *Perplexa* (latin) means confused, intricate, obscure, or ambiguous, and refers to the place where the taxon was observed, Serra das Confusões; it also alludes to its ambiguous generic attribution, and that of its allies.

Diagnostic characters (abbreviations are listed in Appendix 2): A chelid turtle with a shell low: CD/CL = ca. 0.25 (juvenile) – 0.28 (adult) and narrow: CW/CL = ca. 0.7 (juvenile) – 0.6 (adult), laterally constricted in adult. Dorsal scutes noticeably sculpted by both concentric and radiating ridges. Head moderately enlarged

(CW/HW: ca. 3) but with a narrow parietal crest. Temporal and frontal scutes not bulging, with the frontals making a more or less obvious cruciform figure; snout short and pointed, not upturned. Maximum known length: 193.7 mm (female).

Description of the holotype: Shell elongated; horizontal outline elliptical, barely notched at the level of the rear intermarginal sulci; longitudinal outline depressed. Dorsal keel smooth, continuous from V2 to V5. Areolae granular, wide; about five concentric growth rings, made of many small tubercles which draw radiating ridges. Supracaudal scutes subequal to M11. Plastron rather short and narrow; from the longest to the shortest median length of the scutes: intergular, abdominal, anal, femoral, humeral and pectoral. Intergular wider in front, its free border subequal to the gular border. Bridge short, its marginal sulcus curved, with distinct but small axillary (elongated) and inguinal (trapezoidal) scutes. Head flat, wide, and regularly pointed.

Dorsal head scutes well delimited but not protruding, the frontal one making a cross-shaped figure similar to that of *M. gibba*. Skin of the throat slightly granular; two small and short barbels behind the lower rhamphotheca. Neck covered with numerous small, rounded projections, but without elongated or pointed tubercles. Limbs noticeably slender, slightly built. Front aspect of the forearm covered by about 4-5 longitudinal rows of oval, quadrangular or half-moon-shaped scutes, slightly overlapping. Legs with two rows of 4-5 enlarged scutes; the inside ones (fibular) half-moon-shaped, the outside ones (tibial) rather rounded, and the most distal by far the larger.

Coloration: Dorsal aspect regularly dark, the shell brownish, the head, the neck and the limbs dull gray. Under-side lighter; plastron yellowish, with a wide central brown symmetrical patch, extending from the humeral to the femoral, along the bridge, and pointing over the intergular, similar to the ornamentation shown by most

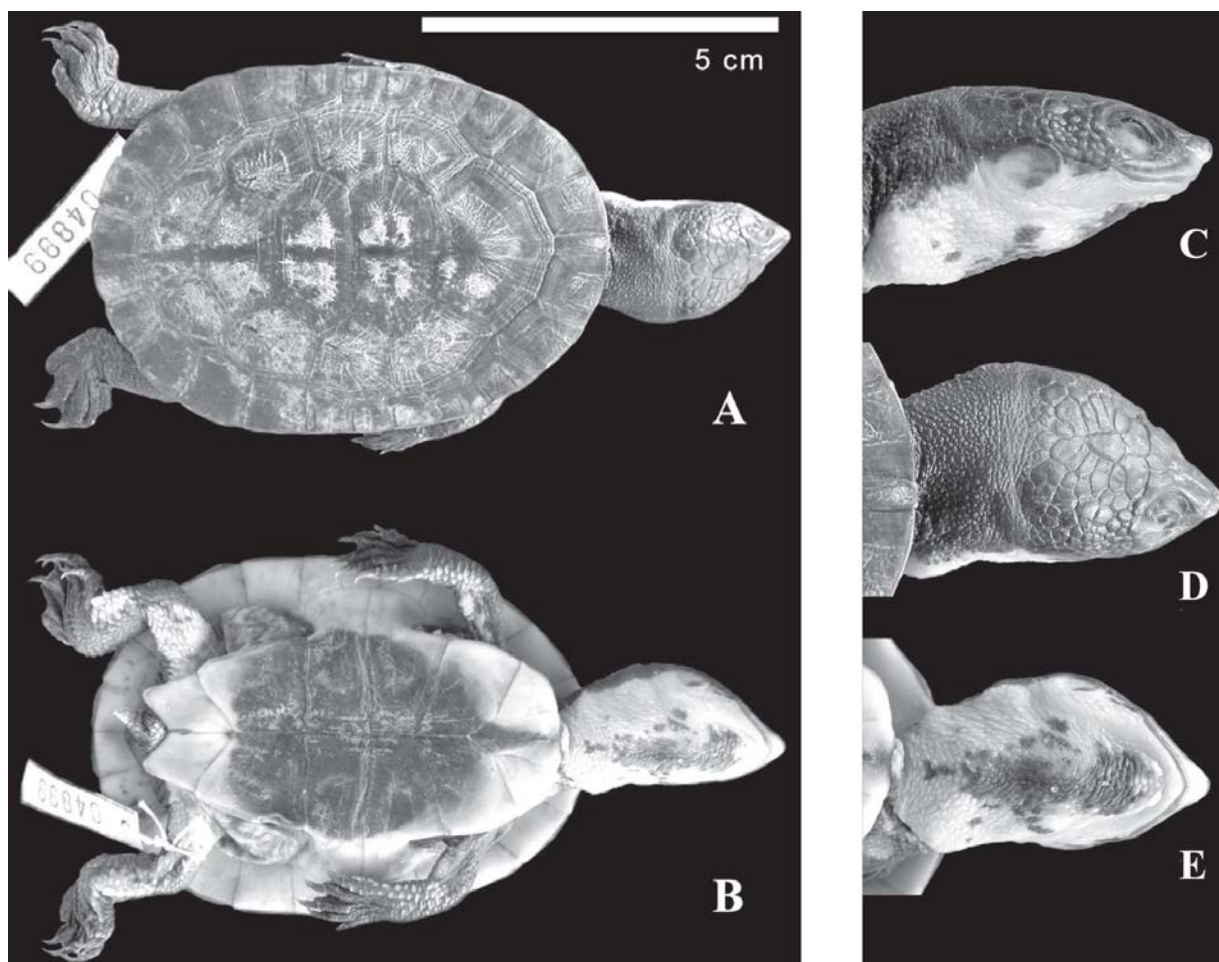


FIGURE 3. Holotype of *Mesoclemmys perplexa* (MZUSP 4111). Dorsal (A) and ventral (B) views of the specimen; lateral (C), dorsal (D), and ventral (E) views of the head.

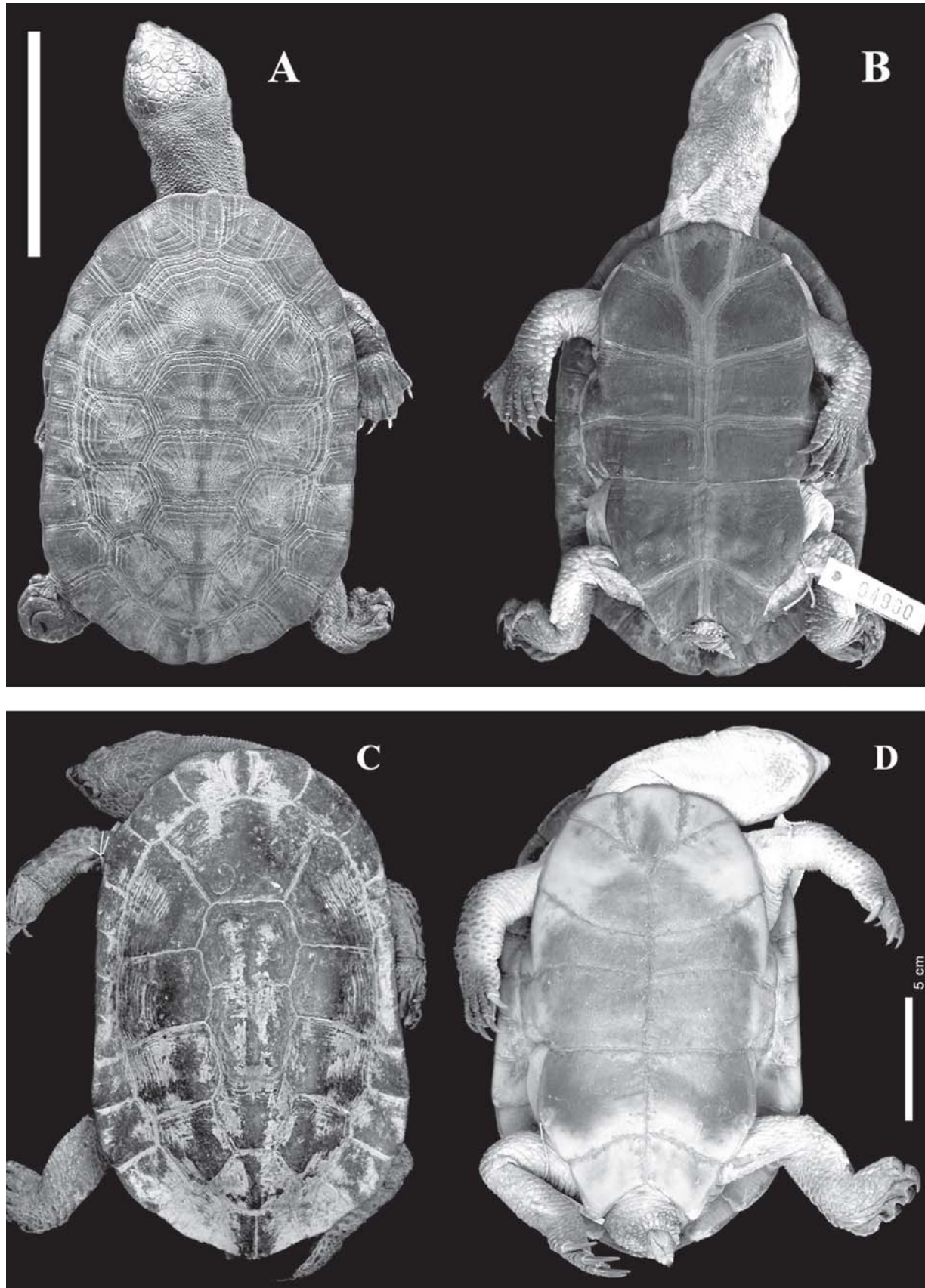


FIGURE 4. Paratypes of *Mesoclemmys perplexa*. Dorsal (A) and ventral (B) views of specimen MZUSP 4112. Dorsal (C) and ventral (D) views of specimen MZUSP 4086.

TABLE 1. Holotype and paratypes of *Mesoclemmys perplexa*: main measurements, with proportions (in relation to the length of the shell).

Carapace length (max.)	CL	<i>Mesoclemmys perplexa</i>					
		MZUSP 4111		MZUSP 4112		MZUSP 4086	
		holotype 67.59 mm		paratype 100.78 mm		paratype 193.65 mm	
		mm	% CL	mm	% CL	mm	% CL
Carapace width (max.)	CW	48.02	0.710	66.80	0.663	115.79	0.598
Carapace depth (max.)	CD	16.70	0.247	25.76	0.256	53.95	0.279
Plastron length (max.)	PM	54.25	0.803	88.41	0.877	163.92	0.846
Plastron length (med.)	PL	51.70	0.765	82.49	0.819	151.20	0.781
Bridge length (min.)	BL	13.84	0.205	21.52	0.214	38.12	0.197
Head width (max.)	HW	15.97	0.236	21.95	0.218	37.45	0.193
Parietal crest width (min.)	PW	0.70	0.010	1.64	0.016	2.59	0.013
Intergular length (med.)	IG	12.24	0.181	19.94	0.198	33.37	0.172
Humeral length (med.)	HU	7.12	0.105	10.91	0.108	25.38	0.131
Pectoral length (med.)	PE	5.51	0.082	11.13	0.110	15.00	0.077
Abdominal length (med.)	AB	9.33	0.138	11.97	0.119	28.25	0.146
Femoral length (med.)	FE	8.36	0.124	16.59	0.165	30.63	0.158
Anal length (med.)	AN	8.77	0.130	11.57	0.115	18.94	0.098
Carapace width / head width	CW/HW	3.007		3.043		3.092	

species of the genus *Mesoclemmys* here recognized (*M. nasuta*, *M. gibba*, *M. heliostemma*, *M. raniceps*, *M. vanderhaegei*, and juvenile *M. tuberculata*). Throat, tympanum and neck whitish, slightly and irregularly mottled with grayish spots; limbs and tail gray with limited whitish areas (arms, thighs, legs, tip of the tail). Laterally, on the head, the limit between the dark and the light areas is sinuous: starting from the nares, it passes through the maxillary horny sheath, then joins the corner of the mouth to the tympanum and follows its upper border. Apparently, the ocular dark stripe is absent.

Differences within the paratypes: MZUSP 4112, L = 100.8 mm: its shell is very similar to the shell of the holotype; outline slightly more sinuous, lateral sides nearly parallel. Plastral median seams lengths are, from longest to shortest: intergular (straight length), femoral, abdominal, anal, pectoral, and humeral. The cruciform frontal figure is poorly delimited. The plastral color pattern is indistinct, covered by a superficial rusty stain. Whitish areas of the soft parts (limbs, neck) not so distinctly delimited; the throat widely covered by grayish spots. MZUSP 4086, L = 193.7 mm: outline distinctly constricted on the sides, partly because of a strong flaring of the posterior marginal scutes. Shell depressed, flat, but proportionally slightly higher than that of the juvenile; dorsal keel smoothed, still obvious on V3 and V4. Plastral median scute lengths are, from the longest to shortest: intergular, femoral, abdominal, humeral, anal, and pectoral; the short anal scutes are probably related to the sex of the specimen. The seam separating the plastron from the marginal

scutes, along the bridge, is deeply grooved, as in *M. gibba*; axillary and inguinal scutes barely distinct. The underside of the marginals, the gular, and the femoral scutes are only slightly washed with a brown tinge, without any obvious dark flecks. Light areas are rather extended on the neck and the limbs; the throat is medially mottled by a patch of small grayish spots; a few similar spots cover the ventral side of the lower jaw.

Comparison with the other species of Mesoclemmys (Appendix 3): *Mesoclemmys perplexa* differs from all other species of *Mesoclemmys* by a narrower and a more depressed carapace, associated with a moderate parieto-squamosal arch and a narrow parietal roof (see Fig. 5). Addi-

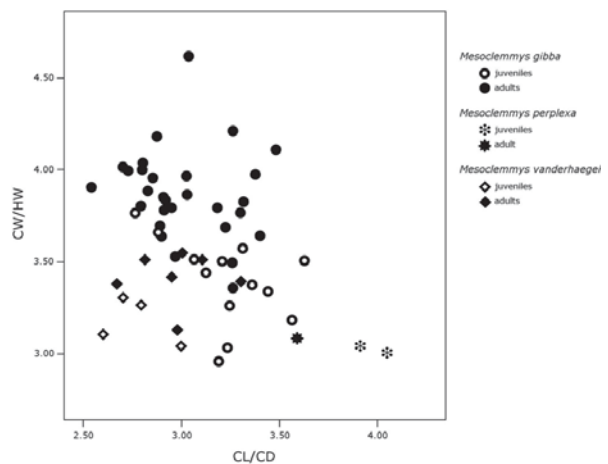


FIGURE 5. Morphometric differences between *Mesoclemmys gibba*, *M. vanderhaegei*, and *M. perplexa*: ratio Carapace length/Carapace depth (CL/CD) versus ratio Carapace width/Head width (CW/HW).

tionally, *M. perplexa* differs from all other species of *Mesoclemmys*, except *M. gibba*, by the presence of a moderate keel in the carapace (a flat or even a medially depressed shell when they age). It differs from *M. dabli*, *M. raniceps*, *M. vanderhaegei*, and *M. zuliae* by the lack of a dark stripe crossing the eye (obvious dark head stripes are present in *M. dabli*, *M. raniceps*, *M. zuliae*; a more or less dark stripe crossing the eye can be observed in *M. dabli*, *M. vanderhaegei*, and *M. zuliae*). *Mesoclemmys perplexa* differs from *M. dabli*, *M. hoguei* and *M. zuliae* by a pigmented plastron. *Mesoclemmys perplexa* differs from *M. hoguei* and *M. vanderhaegei* by the lack of prominent temporal scutes. Finally, it differs from *M. hoguei* by an obviously wider head, thinner barbels, a shorter median abdominal seam. Besides pointing out the identity of *M. perplexa*, this study led to transfer *M. hoguei* and *M. vanderhaegei* from their monotypic genus *Ranacephala* and *Bufocephala*, respectively, to the genus *Mesoclemmys* in its present acceptance. We can notice that Luederwaldt had already proposed this generic attribution to specimens presently identified as *M. hoguei* some 80 years ago (Luederwaldt, 1926:442-443). We also provide in Appendix 3 a discussion of the 19 characters proposed by McCord *et al.* (Appendix B, 2001:750), and their respective character states present in *M. perplexa*.

Quantitative analysis: We also performed a canonical discriminant analysis over seven logarithmized body measurements (maximum carapace width, maximum carapace depth, maximum plastron length, median plastron length, minimum bridge length, and maximum head width) for 18 adult females of the three exter-

nally very similar species *M. perplexa* ($n = 1$), *Mesoclemmys vanderhaegei* ($n = 3$), and *M. gibba* ($n = 14$). Additionally, we performed the same analysis for the 21 juvenile and subadult specimens from both sexes ($n = 2$, $n = 4$, and $n = 15$, respectively). Distances among groups were significant for the adult females (Wilk's ζ , $F = 7.92$, $DF = 14/20$, $p < 0.0001$) and also for juveniles (Wilk's ζ , $F = 5.87$, $DF = 14/26$, $p < 0.0001$ for juveniles). Scores of the specimens on the first and second axes for both analyses are represented in Fig. 6. All statistical analyses were performed using SAS 9.0.

Biological data: Except for its unique biotope and its apparent dependence on perennial water bodies, nothing is known about the eco-ethology of this turtle. The apparent dependence to perennial waterholes, in contrast to the sympatric *M. tuberculata*, together with its isolated and restricted range, suggests that the species exhibits a relictual distribution from a previously wider geographical range established during a much wetter climatic episode of northeastern Brazil.

DISCUSSION

A parsimony analysis was performed using the TNT program (Goloboff *et al.*, 2003) on McCord *et al.*'s (2001) original data matrix with the new species *Mesoclemmys perplexa* included in order to evaluate its phylogenetic position within the taxonomic scheme proposed by these authors (Fig. 7). We reviewed all codings for the 18 characters proposed by McCord

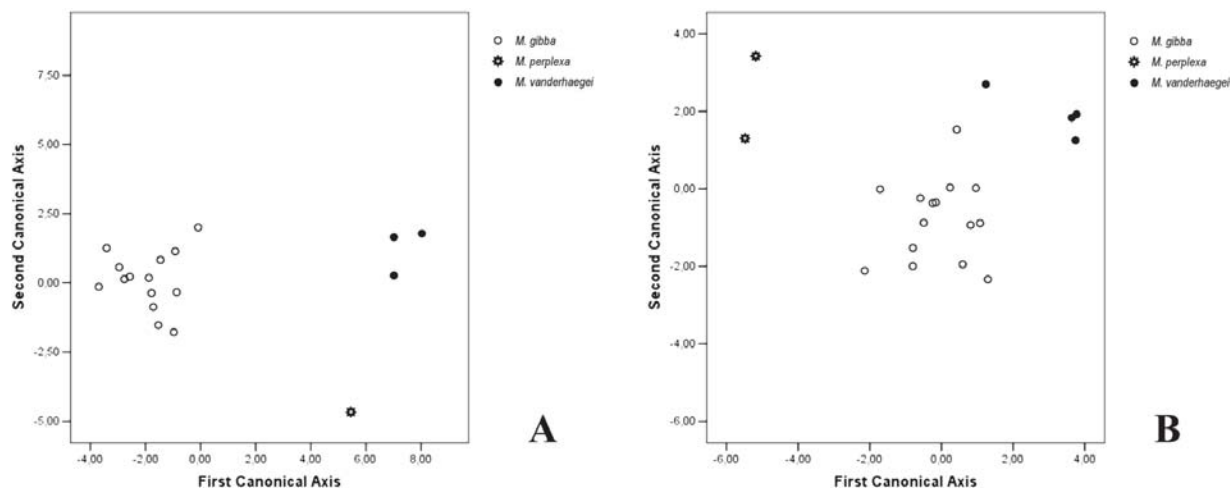


FIGURE 6. Scores of the adult females (A) and juveniles (B) specimens of *Mesoclemmys gibba*, *M. vanderhaegei*, and *M. perplexa* over the first and second axes of the canonical discriminant analysis.

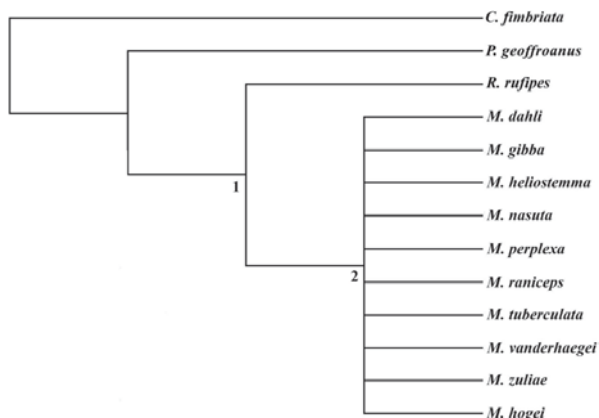


FIGURE 7. Strict consensus tree of the 145 most parsimonious topologies that resulted from a parsimony analysis using TNT, version 1.0. Synapomorphies for the labeled nodes are: Node 1: no unambiguous synapomorphies; ambiguous synapomorphies are 6 (0), 13 (1), 18 (1). Node 2: unambiguous synapomorphies are 8 (1), 9 (1), 17 (1); ambiguous synapomorphies are 3 (0), 4 (1).

et al. (2001), and recoded characters 1, 4, 5, 7, 9, 13, 17, and 18 for *Chelus fimbriata*, *Mesoclemmys gibba*, *M. vanderhaegei*, *M. tuberculata*, *M. hogei*, and *Phrynops geoffroanus*, based on our own observations (see data matrix in Appendix 4). We also added one new character to their data matrix [character 19 – Carapace width in adults with CW/CL superior to 72% (0), equal to 71-68% (1), inferior to 67% (2)]. The character list and data matrix are offered in Appendix 4.

The analysis, implemented using the implicit enumeration (branch and bound) search option, resulted in 145 equally most parsimonious trees with a tree length of 49 steps (all multistate characters non-additive), an ensemble consistency index of 0.49 and a retention index of 0.58. The strict consensus tree supports a basal position of *P. geoffroanus* (Fig. 7) while *Rhinemys rufipes* appears as the sister-taxon to a clade formed by the remaining ‘toad-headed’ species, as previously suggested by McCord *et al.* (2001). On the other hand, the present analysis does not support the phylogenetic hypothesis suggested by McCord *et al.* (2001) for the remaining ‘toad-head’ turtles, the latter clade corresponding to a polytomy including their *Mesoclemmys gibba*, *Bufocephala vanderhaegei*, *Ranacephala hogei*, *Batrachemys dahl*, *B. heliostemma*, *B. nasuta*, *B. raniceps*, *B. tuberculata*, and *B. zuliae*, and the new species described in the present study (Fig. 7). Additionally, both clades are only weakly supported, with bootstrap percentages inferior to 50% and a Bremer support of one. These results suggest that the taxonomic scheme proposed by McCord *et al.* (2001) for the ‘toad-headed’ South American chelids, with the recognition of five

new genera including two new ones, is not appropriate respect to the present knowledge of the group. In that sense, the more conservative approach used here (i.e., including these species in the older genus *Mesoclemmys*) represents a better solution until a well supported hypothesis of relationships is proposed for the ‘toad-headed’ South American chelids.

RESUMO

Uma nova espécie de cágado pleurodira é descrito do estado do Piauí, Brasil. Esta se aparenta com as espécies amazônicas do gênero Mesoclemmys s.l. (nova aceção) e pode ser considerada como uma população biogeograficamente relictual de uma espécie que vivia outrora sob um clima mais úmido no nordeste brasileiro.

PALAVRAS-CHAVE: Chelonii, Chelidae, sistemática, taxonomia, filogenia, *Mesoclemmys perplexa*, espécie nova, Piauí, Brasil.

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APPENDIX 1

New taxonomic arrangement adopted in the present study for the species formerly recognized as belonging to the genus *Phrynops* sensu lato.

***Phrynops* Wagler, 1830**

Type species: by monotypy: *Emys geoffroana* Schweigger, 1812.

Contents: *Phrynops geoffroanus* (Schweigger, 1812); *Phrynops bilarii* (Duméril & Bibron, 1835); *Phrynops williamsi* Rhodin & Mittermeier, 1984. Systematics of *P. geoffroanus* and its allies is presently not totally satisfying and needs a revision.

***Rhinemys* Wagler, 1830**

Type species: by subsequent designation: *Emys rufipes* Spix, 1824.

Contents: *Rhinemys rufipes* (Spix, 1824).

***Mesoclemmys* Gray, 1863**

Type species: by monotypy: *Emys gibba* Schweigger, 1812.

Synonyms: *Batrachemys* Stejneger, 1909 (type species, by original designation: *Emys nasuta* Schweigger, 1812); *Bufocephala* McCord *et al.*, 2001 (type species, by original designation: *Phrynops vanderhaegei* Bour, 1973); *Ranacephala* McCord *et al.*, 2001 (type species, by original designation: *Phrynops hoguei* Mertens, 1970).

Contents: *Mesoclemmys dabli* (Zangerl & Medem, 1958), comb. nov.; *Mesoclemmys gibba* (Schweigger, 1812); *Mesoclemmys heliostemma* (McCord, Joseph-Ouni & Lamar, 2001), comb. nov.; *Mesoclemmys hoguei* (Mertens, 1970), comb. nov.; *Mesoclemmys nasuta* (Schweigger, 1812), comb. nov.; *Mesoclemmys perplexa* sp. nov.; *Mesoclemmys raniceps* (Gray, 1855), comb. nov.; *Mesoclemmys tuberculata* (Luederwaldt, 1926), comb. nov.; *Mesoclemmys vanderhaegei* (Bour, 1973), comb. nov.; *Mesoclemmys zuliae* (Pritchard & Trebbau, 1984), comb. nov.

APPENDIX 2**Abbreviations.**

AB: Abdominal length

AN: Anal length

BL: Bridge length

CD: Carapace depth

CL: Carapace length

CW: Carapace width

FE: Femoral length

HU: Humeral length

HW: Head width

IG: Intergular length

M: Marginal scute

MNHN: Muséum national d'Histoire Naturelle, Paris

MZUSP: Museu de Zoologia da Universidade de São Paulo

N: Neural plate (bone)

NMW: Naturhistorisches Museum, Wien

NHM: Natural History Museum, London (ex BMNH)

PE: Pectoral length

PL: Plastron length (medial)

PM: Plastron length (maximum)

PW: Parietal crest width

SMF: Senckenberg Museum, Frankfurt

V: Vertebral scute

ZSM: Zoologisches Staatssammlung, München

APPENDIX 3

Character states present in *Mesoclemmys perplexa* following the list of 19 characters and their states as proposed by McCord *et al.* (Appendix B, 2001:750), completed and modified.

1) Color of head (and eye stripe):

Dark gray, very slightly mottled with beige; whitish areas on the edge of the upper jaw, on the lower jaw, on the barbels, under and behind the tympanum, on the lower part of the neck; throat more or less extensively speckled with gray. There is no dark stripe crossing the eye.

A dark head, uniform or mottled with beige, with lighter undersurfaces, is also observed in *M. gibba*, *M. bogei*, *M. nasuta*, *M. tuberculata*, *M. vanderhaegei*. At least one obvious dark head stripe is present on the temporal area of *P. geoffroanus* and its allies, *R. rufipes*, *M. dabli*, *M. raniceps*, *M. zuliae*. A more or less dark stripe crossing the iris of eye can be observed in *P. geoffroanus* and its allies, *M. dabli*, *M. vanderhaegei*, and *M. zuliae*.

2) Size of head relative to carapace:

Moderate, HW/CL = 23.6, 21.8 and 19.3% (young to adult). However, in connection with the narrow shell, the head looks wide.

M. gibba exhibits similar proportions. Narrower heads are typical of *P. geoffroanus* and above all *M. bogei*. A wider head is observed in *M. vanderhaegei* and especially in all the members of the former *Batrachemys* group.

3) Flatness of head:

Fairly flat; scales well delimited by deep grooves, temples slightly bulging on the adult.

This character is somewhat subjective. See Appendix 4 for the McCord *et al.*'s interpretation. Prominent temporal scutes are especially conspicuous in *M. bogei* and *M. vanderhaegei*.

4) Shape of head:

Rather short, pointed, eyes oriented laterally.

Same remark as above, a character which is somewhat subjective, and partly correlated with the widening of the head.

5) Snout:

Pointed, not upturned.

Only *P. geoffroanus* has a distinct 'blunt' head.

6) Length of barbels:

Short barbels.

Only *P. geoffroanus* and its allies (notably *P. bilarii*) have obviously elongated barbels. *M. bogei* has no elongated barbels, but they are thick and look large because of the small head.

7) Parietal roof:

Narrow, PW/HW = ca. 7%.

An evolutive character in this group, closely associated with character (2). The primitive condition seems to be that observed in the genus *Acanthochelys* Gray, 1873, closely related to *Mesoclemmys*. A slight reduction occurs in *R. rufipes* and *P. geoffroanus*. A further shrinking appears in *M. bogei* and *M. gibba*, next in *M. vanderhaegei* and finally in the members of the former *Batrachemys* genus. Moreover, there is an ontogenetic increasing of this character.

8) Parieto-squamosal arch:

Moderate as determined by X-ray views.

A feature also probably associated with character (2)

9) Number of neural bones:

Apparently none, from an X-ray plate of MZUSP 4086.

An individually variable character. A tendency to a reduction of the neural bones (from 5 to 0, with disappearance of the first one, N1) is documented for all species, except for *R. rufipes*, for *P. geoffroanus* and its allies, and for *Chelus*.

10) Presence of first neural:

Apparently absent.

Cf. above, character (9). N1 is present in *P. geoffroanus* and its allies, also in *Chelus fimbriata*.

11) Width of intergular scute compared to gulars (at anterior plastron):

Intergular border subequal or wider than gular border.

A rather variable character (cf., for instance, *R. rufipes*), without a great evolutive significance. See Appendix 4 for the McCord *et al.*'s interpretation.

12) Plastral seam formula:

With long IG, AB and FE, short HU and PE, quite variable AN; IG>AB>AN>FE>HU>PE (juvenile); IG>FE>AB>AN>PE>HU (subadult); IG>FE>AB>HU>AN>PE (adult female).

This character is here significative to segregate *M. hoguei*, of which the median abdominal seam is the longest.

13) Depth of carapace:

Flat.

M. perplexa has a really depressed shell, apparently unique at the young age among the studied group. We have quantified the depth, CD/CL Ø33% being high shells, CD/CL < 33% being low shells. The proportionnaly highest shells are those of *M. gibba*, *M. vanderhaegei*, and *M. tuberculata*, and the tectiform one of *R. rufipes*. Lowest shells are those of *M. perplexa* (28%, one adult female), and of some *M. hoguei*, *M. nasuta*, *M. raniceps* and probably *M. heliostemma* (being slightly under 29%).

14) Presence of carapacial keel:

Yes, moderate, smooth.

A slightly stronger keel, broken off, is typical of *M. gibba*. Other adult members of the group have a flat or even a medially depressed shell when they age. The tectiform shell of *R. rufipes* is quite peculiar.

15) Presence of median groove in carapace:

No; but lateral (paramedial) shallow grooves in adult.

Cf. above. The depth of the groove of the old specimens may vary individually.

16) Width of 11th marginals (measured side to side, or intermarginal seam to intermarginal seam) compared to supracaudals:

11th and 12th marginal scutes subequal.

A character probably without a great evolutive significance. See Appendix 4 for the McCord *et al.*'s results.

17) Large distal scale medial tibial row of scales:

Yes, about twice the size of the adjoining scale.

Obviously just a specific character. See Appendix 4 for the McCord *et al.*'s results.

18) Upturned lateral borders of carapace:

A slight lateral constriction in the adult male.

This character is significative to segregate *P. geoffroanus*, which has no upturned lateral borders. *M. hoguei* is said to also have no such folded lateral marginals, but Luederwaldt (1926:443; pl.) described and figured a specimen of *M. hoguei* with a "Carapaça, nos bordos lateraes, levantada para cima..." (his specimen number 96).

19) Plastral pattern:

A yellowish background with a large central dark (brown to blackish) area, covering most of the scutes between humerals and femorals, extending medially on the intergular, but not on the bridges; underside of marginals yellow.

As said above in the text, this peculiar color pattern is shown by most species of the genus *Mesoclemmys* here recognized (*M. nasuta*, *M. gibba*, *M. belioSTEMMA*, *M. raniceps*, *M. tuberculata*, *M. vanderhaegei*). *M. bogei*, *M. dahl*i and *M. zuliae* have a nearly uniformly yellow plastron, probably a secondary evolution. With age *M. tuberculata* pattern fades, and there is a secondary dark pigmentation along the seams. *P. geoffroanus* and its allies have a spotted pattern, which may fade with the age.

20) Width of the shell (CW/CL):

Shell outstandingly narrow, both in the young (71%) and the adult female (60%). This is quite obvious, because the shell is also depressed.

All other compared turtles have a wider shell, the narrowest shells of adult being those of *M. bogei*, *M. vanderhaegei* and *M. zuliae* (ca. $69 \pm 3\%$). Widest shells (mean ca. $76\% \pm 3\%$) are found in *R. rufipes* and *M. nasuta*.

APPENDIX 4

Character list and data matrix adapted and modified from McCord *et al.* (2001), and used in the present study. Character numbering used by these authors is given in parenthesis. Character 19 and the new taxon *Mesoclemmys perplexa* were added to their matrix. A third state (“plastron with spots and flecks”) was added to character 18. Changed states with regard to the original data matrix used by McCord *et al.* (2001) are typed in bold face.

- 01 (#2) – Head size: small = 0; medium = 1; broad = 2
 02 (#3) – Flatness of head: flat = 0; rounded = 1;
 03 (#4a) – Head width (HW/HL): 80-90% = 0; > 90% = 1
 04 (#4b) – Eye orientation: laterally = 0; dorsally = 1
 05 (#5) – Snout: blunt = 0; pointed = 1
 06 (#6) – Barbels: small = 0; long = 1;
 07 (#7) – Parietal roof width: wide, > 20% = 0; medium, 15-20% = 1; narrow, < 13% = 2
 08 (#8) – Parieto-squamosal arch: substantial = 0; medium = 1; narrow = 2
 09 (#10) – Neural series: first neural reaches preneural (nuchal) = 0; not = 1
 10 (#11) – Intergular/gular width: intergular wider or equal to gulars = 0; intergular narrower = 1
 11 (#12a) – Intergular vs interabdominal seam: IG > IAB = 0; IAB > IG = 1
 12 (#12b) – Interanal vs interpectoral seams: IAN > P = 0; IP > IAN = 1
 13 (#13) – Shell depth: low shell = 0; medium to high domed = 1
 14 (#15) – Carapacial median groove: no groove = 0; present = 1
 15 (#16) – 11th and 12th marginal widths: 11th > 12th = 0; Equal = 1; 12th > 11th = 2
 16 (#17) – Distal tibial scale: well developed = 0; moderatel to poorly developed = 1
 17 (#18) – Upturning of lateral margin of carapace: not upturned = 0; upturned = 1
 18 (#19) – Plastron coloration: wide median dark patch = 0; yellow only = 1; spots and flecks = 2
 19 – Shell width, adults (CW/CL): Ø72% = 0; between 71-68% = 1; ~~Ø67%~~ = 2

DATA MATRIX

Characters	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
Characters in McCord <i>et al.</i>	#2	#3	#4a	#4b	#5	#6	#7	#8	#10	#11	#12a	#12b	#13	#15	#16	#17	#18	#19	
<i>C. fimbriata</i>	2	0	1	0	1	1	0	0	0	0	0	1	0	0	1	1	0	2	2
<i>M. dahl</i>	2	1	0	1	1	0	2	2	1	0	0	1	0	1	1	1	1	1	0
<i>M. gibba</i>	1	0	0	1	1	0	0	1	1	0	0	0	1	0	2	1	1	0	0
<i>M. heliostemma</i>	2	1	0	1	1	0	2	1	1	1	0	1	0	1	0	0	1	0	0
<i>M. nasuta</i>	2	1	0	1	1	0	2	2	1	0	0	0	0	1	1	0	1	0	0
<i>M. perplexa</i>	1	0	1	1	1	0	2	1	1	0	0	0	0	0	1	0	1	0	2
<i>M. raniceps</i>	2	1	0	1	1	0	2	2	1	0	0	1	0	1	1	0	1	0	1
<i>M. tuberculata</i>	2	1	0	1	1	0	2	2	1	1	0	0	1	1	1	0	1	0	1
<i>M. vanderhaegei</i>	2	1	0	1	1	0	2	1	1	0	0	0	1	1	2	1	1	0	1
<i>M. zuliae</i>	2	1	0	1	1	0	2	2	1	0	0	0	0	1	1	0	1	1	1
<i>M. bogei</i>	0	0	0	0	1	1	0	1	1	1	1	0	1	1	2	0	1	1	1
<i>R. rufipes</i>	1	0	1	0	1	0	0	0	0	0	0	0	1	0	2	1	0	1	0
<i>P. geoffroanus</i>	0	0	1	0	0	1	0	0	0	1	0	0	0	1	0	1	0	2	0

APPENDIX 5

Specimens examined.

We have studied and most often have taken measurements of specimens kept in the collections of the following museums: MNHN, MZUSP, NHM, NMW, SMF and ZSM. Beside we have observed, or got the measurements, of living specimens in the collections of 'A Cupulatta' (Cédric Coutard and Philippe Magnan) = AC, of William McCord = WM, of Sébastien Métrailler = SM, and of Ingo Pauler = IP.

Phrynops geoffroanus: 10 specimens (MNHN, NHM), including holotypes of *Emys geoffroana* (MNHN 9417) and of *Platemys nagleri* (MNHN 8758).

Phrynops hilarii: 30 specimens (AC, MNHN, NHM), including holotypes of *Platemys hilarii* (MNHN 8757), *Spatulemys lasalai* (NHM 1947.3.5.93), and *Hydraspis boulengeri* (NHM 1947.3.5.94).

Phrynops tuberosus: 7 specimens (AC, IP, NHM).

Phrynops williamsi: 4 specimens (AC, MNHN).

Rhinemys rufipes: 1 specimen, the holotype (ZSM 3006/0); we have used published data by Lamar & Medem, 1983.

Mesoclemmys dahli: 2 specimens (IP, SMF), topotypes.

Mesoclemmys heliostemma: 1 specimen, paratype (NHM 1904.7.26.1).

Mesoclemmys gibba: 60 specimens (AC, IP, MNHN, NHM, SM, WM), including holotypes of *Emys gibba* (MNHN 8756), *Platemys miliusii* (MNHN 8755), *Hydraspis gordonii* (NHM 1947.3.4.18), and *Hydraspis bicolor* (NHM 1946.1.22.86).

Mesoclemmys hoguei: 4 specimens (MZSUP, SMF), including the holotype of *Phrynops hoguei* (SMF 62530).

Mesoclemmys nasuta: 8 specimens (AC, MNHN, NHM), including the holotype of *Emys nasuta* (MNHN 4140).

Mesoclemmys perplexa: 3 specimens (MZUSP), one holotype and two paratypes.

Mesoclemmys raniceps: 15 specimens (IP, MNHN, NHM, NMW), including lectotype of *Hydraspis raniceps* (NHM 1947.3.5.92), holotype of *Hydraspis maculata* (NHM 1946.1.22.14) and paratype of *Phrynops wermuthi* (IP, now deposited as SMF 66247).

Mesoclemmys tuberculata: 6 specimens (IP, MNHN, MZUSP), including the lectotype of *Rhinemys tuberculata* (MZUSP 43).

Mesoclemmys vanderhaegei: 12 specimens (IP, MNHN), including the holotype of *Phrynops tuberculatus vanderhaegei* (MNHN 1977.50)

Mesoclemmys zuliae: 2 specimens (MNHN, IP), topotypes.